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ORIGINAL ARTICLE

Ecological responses to forest age, habitat, and host vary by mycorrhizal type in boreal peatlands

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Abstract

Despite covering vast areas of boreal North America, the ecological factors structuring mycorrhizal fungal communities in peatland forests are relatively poorly understood. To assess how these communities vary by age (younger vs. mature), habitat (fen vs. bog), and host (conifer trees vs. ericaceous shrub), we sampled the roots of two canopy trees (*Larix laricina* and *Picea mariana*) and an ericaceous shrub (*Ledum groenlandicum*) at four sites in northern Minnesota, USA. To characterize the specific influence of host co-occurrence on mycorrhizal fungal community structure, we also conducted a greenhouse bioassay using the same three hosts. Root samples were assessed using Illumina-based high-throughput sequencing (HTS) of the ITS1 rRNA gene region. As expected, we found that the relative abundance of ectomycorrhizal fungi was high on both *Larix* and *Picea*, whereas ericoid mycorrhizal fungi had high relative abundance only on *Ledum.* Ericoid mycorrhizal fungal richness was significantly higher in mature forests, in bogs, and on *Ledum* hosts, while ectomycorrhizal fungal richness did not differ significantly across any of these three variables. In terms of community composition, ericoid mycorrhizal fungi were more strongly influenced by host while ectomycorrhizal fungi were more influenced by habitat. In the greenhouse bioassay, the presence of *Ledum* had consistently stronger effects on the composition of ectomycorrhizal, ericoid, and ericoid-ectomycorrhizal fungal communities than either *Larix* or *Picea*. Collectively, these results suggest that partitioning HTS-based datasets by mycorrhizal type in boreal peatland forests is important, as their responses to rapidly changing environmental conditions are not likely to be uniform.

Keywords Mycorrhizal fungi · Bog · Fen · *Larix laricina* · *Picea mariana* · *Ledum groenlandicum* · SPRUCE

Introduction

Peatland forests cover vast areas of the boreal North America (Wieder and Vitt 2006). These areas are characterized by high water tables, which favors the growth of peat-forming *Sphagnum*. Although the accumulation of peat makes these habitats globally important as carbon sinks (Gorham 1991), plant species richness is typically low, with only a handful of conifers, ericaceous shrubs, and graminoids present (Wright et al. 1992). The structure of peatland forest vegetation is spatially heterogeneous and strongly associated with local hydrologic conditions (Heinselsman 1970). In bogs, where water comes from rain or snow rather than groundwater inputs, pH and nutrient availability are both low. As such, the bogs in boreal North American peatland forests are characterized by thick ericaceous shrub understory and *Picea mariana* as the dominant canopy tree. In contrast, in fens, where springs or streams are the primary water sources, there is less acidity and richer nutrient conditions. The fens in North America have a correspondingly higher density of *Larix laricina* as the dominant canopy tree and lowered presence of ericaceous shrubs. In terms of succession, peatland forests transition from fens to bogs (and thus from *L. laricina* to *P. mariana* and more ericaceous shrubs in North America), with fire facilitating conifer re-establishment by removing the thick

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soil organic layer (i.e., peat) that develops over time (Johnstone and Chapin 2006; Collier and Mallik 2010).

While the structure and dynamics of the vegetation in peatland forests are relatively well understood, much less is known about the fungal communities present in these forests. Globally, culture- and sporocarp-based estimates of fungal diversity in peatlands are in the hundreds of species (Thormann and Rice 2007), but recent molecular studies suggest these communities may be even richer (Sun et al. 2016; Asemaninejad et al. 2017; Hiiesalu et al. 2017). The composition of the fungal communities in peatland forests appears to be affected by ecological factors similar to those in adjacent upland habitats, although community composition is often notably different (Wurzburger et al. 2004; Hiiesalu et al. 2017). For example, in a Finnish peatland forest, Sun et al. (2016) found that peatland soil fungal community composition was significantly influenced by which ectomycorrhizal host tree species was locally dominant and that human-caused alteration of hydrological conditions also modified fungal community structure. Microscale habitat variation has also been shown to be important, as Asemaninejad et al. (2017) found that hummocks (i.e., raised areas of peat) harbored significantly richer fungal communities than adjacent hollows (i.e., areas of peat closer to the water table). Despite these recent insights, how the fungal communities in peatland forests vary at larger spatial and temporal scales (e.g., between fens and bogs or between younger and mature forests) remain poorly described, particularly using high throughput sequencing methods that can more accurately capture the high diversity present in most fungal communities (Peay et al. 2016).

The positioning of peatland forests in North America at high latitudes also makes these forests particularly susceptible to altered environmental conditions associated with climate change (Serreze et al. 2000). In particular, these forests are experiencing a greater degree of temperature warming compared to forests at lower latitudes, which has been previously shown to inhibit the performance of cold-adapted plant species (Reich et al. 2015). Altered plant performance due to warming has been shown to have significant effects on root-associated fungal communities, particularly mycorrhizal fungi (Clemmensen et al. 2006; Deslippe et al. 2011), which result in feedbacks that may further alter vegetation structure (Fernandez et al. 2017). Although there is growing interest in understanding fungal responses to climate change (Mohan et al. 2014), basic knowledge about mycorrhizal fungal community distributions along different ecological niche axes such as forest age, habitat, and host in peatland forests is still limited. In particular, there has been no specific focus on determining whether different types of mycorrhizal fungi (e.g., ectomycorrhizal vs. ericoid) have similar or contrasting responses to shared ecological niche axes.

To investigate how the mycorrhizal fungal communities in peatland forests in North America vary by age, habitat, and host, we conducted a field sampling in northern Minnesota of two canopy trees (*Larix laricina* and *Picea mariana*) and an ericaceous shrub (*Ledum groenlandicum*). We used a high-throughput amplicon sequencing approach (a.k.a. DNA "metabarcoding") to characterize the mycorrhizal fungal communities present on roots of different hosts from fen and bog habitats as well as peatland forests of different ages. Although this correlative approach can help determine the relative importance of various ecological factors, because both abiotic conditions and host dominance change across habitats, experimental assays are needed to better understand how the co-occurrence of different hosts affects mycorrhizal fungal community structure. This is particularly important in regard to assessing the specific effects of ericaceous shrubs, which are known to produce allelopathic substances that inhibit ectomycorrhizal host recruitment (Mallik 2003). Thus, to address how host neighborhood effects influence mycorrhizal community richness and composition, we also conducted a greenhouse bioassay involving all single, two-, and three-way combinations of the three hosts sampled in the field study. We hypothesized that the richness and relative abundance of ectomycorrhizal (ECM) and ericoid (ERM) mycorrhizal fungal communities would correspond with known host abundances. Further, we predicted that both forest age and habitat would significantly influence mycorrhizal community composition but that the effects may be greater for ECM than ERM fungi, given their greater species diversity and higher host specificity. Finally, in the greenhouse bioassay, we expected that the presence of *Ledum* would significantly alter the richness and composition of *Picea* and *Larix* ECM fungal communities but that the effects would be lower in the three- than either two-host combination.

Materials and methods

Field sampling

The field sampling was conducted at the Marcell Experiment Forest, approximately 40 km north of Grand Rapids, Minnesota, USA (47° 30.17′ N, 93° 28.97′ W). This area is characterized by a boreal climate, with extended cold winters and cool summers (mean annual temperature = 8.3 °C, mean annual range = − 2.7–19.4 °C, mean annual precipitation = 2.4 cm as rain and 33 cm as snow). The south unit of Marcell contains multiple bogs and fens that have been the subject of long-term ecological research of peatland hydrology and ecology (Kolka et al. 2011). Our sampling targeted four of those sites, S1, S2, S3, and S6, which are located ~ 1–5 km apart from one another (https://www.nrs.fs.fed.us/ef/marcell/sites/). The S1 site is a bog that was logged in 1972 and the current location of the Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment

(Hanson et al. 2017). We sampled an area of the bog 50–150 m north of the SPRUCE experiment where there has been no disturbance associated with the project, but the vegetational composition, hydrology, and edaphic factors are very similar. Vegetation in the S1 bog consists of a nearly equal mix of *Larix laricina* and *Picea mariana* as the only tree species, and a rich ericaceous shrub layer in which *Ledum groenlandicum* (a.k.a. *Rhododendron groenlandicum*) is very common. The S2 bog site consists of a more mature monodominant *Picea mariana* canopy and abundant *Ledum groenlandicum* in the ericaceous understory that naturally established following a major fire in 1864. The S3 site, which is immediately south of the more well-studied S3 fen, was established after logging in 1972 and consists of a low-density monodominant canopy of *Larix*, a very limited presence of *Ledum groenlandicum* and no *Picea mariana* individuals. Lastly, the S6 bog also naturally established following the 1864 fire and consists of a nearly equal mix of *Larix laricina* and *Picea mariana* as the only tree species along with abundant *Ledum groenlandicum* in the ericaceous understory.

We visited Marcell Experimental Forest in May 2015 to conduct our field sampling (Fig. S1). At each site, we took 10 samples from each host when possible (S1: 10 *Larix*, 10 *Picea*, 10 *Ledum*; S2: 10 *Picea*, 10 *Ledum*, S3: 10 *Larix*, 2 *Ledum*, S6: 10 *Larix*, 10 *Picea*, 10 *Ledum*). Individual sets of samples of the hosts (triplicates or pairs depending on host presence) were taken within two meters of each other, to maximize the potential for the root systems of the different hosts to overlap, which has been previous shown to play an important role in host specificity patterns (Bogar and Kennedy 2013). Sets of samples within each site were located at least 10 m apart to ensure spatial independence (Tedersoo et al. 2010). Root samples were collected by pushing back the upper peat layer, visually searching for roots, and then taking bulk collections of root-containing peat from a ~ 1000 cm^3 volumes. Samples were placed in sterile plastic bags and transported on ice back to the laboratory the same day. Within 48 h, roots were carefully separated from adhering peat by multiple washings in tap water. Cleaned roots were then sorted by host based on macromorphology (Fig. S2) and dried at 40 °C for 36 h. Once dried, the roots were stored in envelopes at room temperature prior to molecular analysis.

Greenhouse bioassay

In June 2015, we established a bioassay at the University of Minnesota growth facilities (hereafter greenhouse) to further examine the effects of host co-occurrence on mycorrhizal fungal community structure. For this assay, we purchased 12 month nursery grown seedlings of *Larix laricina* and *Picea mariana* from the Minnesota Department of Natural Resources (Akeley, MN, USA) and ~ 8-year *Ledum groenlandicum* shrubs from a nursery in Washington State, USA (Keeping it Green Nursery, Standwood, WA). We first carefully removed all soil from the root systems for each seedling and shrub and then planted the three hosts into seven different treatment combinations: (1) *Larix* alone, (2) *Picea* alone, (3) *Ledum* alone, (4) *Larix* and *Picea*, (5) *Larix* and *Ledum*, (6) *Picea* and *Ledum*, and (7) *Larix*, *Picea*, and *Ledum*. The seedlings were planted into 4-L plastic pots containing a 2:1 mix of sterilized peat moss and potting soil. To provide a local source of mycorrhizal inoculum, we sampled similarly sized clumps of root-containing peat (6 cm × 6 cm × 6 cm) from Beckman Bog at the Cedar Creek Ecosystem Science Reserve (45° 25.455′ N, 93° 11.113′ W, East Bethel, MN, USA). Equal amounts of this inoculum were added into each pot next to the roots of the host plants. Treatments were replicated five times and watered consistently to maintain high soil moisture content. In January 2016 (experiment duration = ~ 7 months, greenhouse temperature = 23.8 °C (day) to 12.8 °C (night)), all plants were removed and their roots were carefully sorted using the same methods as in the field sampling. There was some mortality in the experiment, so the final sample sizes by host treatment were: *Larix* alone = 5, *Picea* alone = 4, *Ledum* alone = 5, *Larix* and *Picea* = 4, *Larix* and *Ledum* = 4, *Picea* and *Ledum* = 5, and *Larix*, *Picea*, and *Ledum* = 3.

Molecular analyses

To identify the mycorrhizal fungi present on *Larix, Picea, and Ledum* roots, whole roots from each sample was first gently crushed inside of their storage envelopes to separate smaller mycorrhizal colonized roots from the larger non-colonized coarse roots. Twenty milligrams of the smaller fine root portion was placed in screw-cap tubes with glass beads and homogenized for 1 min via bead beating at continuously variable shaking speeds of 2000–3450 strokes per minute (BioSpec Products, Bartlesville, OK, USA). Total genomic DNA was extracted from each homogenized root sample independently using a standard CTAB-chloroform extraction method detailed in Kennedy et al. (2003). ITS1 rDNA was PCR amplified for each sample using a barcoded fungal-specific ITS1F-ITS2 primer set (Smith and Peay 2014) using a Hot Start Taq polymerase with proofreading capability. Annealing temperatures were set to 54 °C and cycled 30 times. Amplified products were cleaned using the Charm "Just-A-Plate" cleanup kit (Charm Biotech, San Diego, CA, USA) and quantified using a Qubit 2.0 dsDNA HS Fluorometer (Life Technologies, Carlsbad, CA, USA). Individual field and greenhouse libraries were pooled at equimolar concentration and sequenced at the University of Minnesota Genomics Center using the 2 × 250 bp paired-end MiSeq Illumina platform. Raw sequences and associated metadata were deposited in the NCBI Short Read Archive (BioProject #: PRJNA430245).

Fungal sequences were processed using the FAST pipeline version 1.102 (https://github.com/ZeweiSong/FAST). After demultiplexing, primers were trimmed using Cutadapt (Martin 2011), forward and reverse reads were paired using PEAR (Zhang et al. 2013), and the SSU and 5.8S gene regions were removed. Low-quality sequences were removed using the criteria maximum expected error rate = 1 and singletons discarded following dereplication. Chimeras were detected and eliminated using VSEARCH (https://github.com/torognes/vsearch) and the UNITE v7.1 database (Kõljalg et al. 2013). The remaining sequences were clustered into operational taxonomic units (OTUs) at 97% similarity using the VSEARCH greedy algorithm. To remove possible non-fungal OTUs, only those matching the UNITE database at 75% match over 70% of their length were retained (as in Tedersoo et al. 2014). Taxonomy was assigned using VSEARCH. Following the recommendation of Lindahl et al. (2013), all cells in this initial OTU × sample matrix with less than three reads were zeroed.

Mycorrhizal fungal OTUs were separated from those belonging to other fungal guilds using the online tool FUNGuild (Nguyen et al. 2016, www.funguild.org). For the mycorrhizal OTU × sample matrix, we included all OTUs that FUNGuild assigned as having a "highly probable" and "probable" likelihood of being an arbsucular mycorrhizal (AM), ectomycorrhizal (ECM), or ericoid (ERM) mycorrhizal fungal taxon. We also included a fourth category for mycorrhizal OTUs that are known to colonize both ericoid and ectomycorrhizal hosts (hereafter referred to ericoid-ectomycorrhizal, ERM-ECM). For all OTUs that had a "possible" mycorrhizal designation, we checked the species-level matches and removed any OTU that matched more closely to non-mycorrhizal than mycorrhizal fungal sequences. Among the OTUs that were unassigned in FUNGuild, we determined that some were likely mycorrhizal despite not being assigned to that guild (due to missing family- and/or genus-level taxonomy). We therefore checked the individual UNITE database species hypotheses (SH in Kõljalg et al. 2013) for the 49 unassigned OTUs with sequence read abundances over 5000 reads (which represented 90% of all unassigned sequences). We were able to reassign 28 of the 49 OTUs to one of three dominant mycorrhizal types (ECM, ERM, or ERM-ECM), which combined with assigned OTUs, totaled 90% of all sequences passing quality filtering. The resulting mycorrhizal fungal OTU × sample matrices, which include both taxonomic identification and mycorrhizal type assignment for each OTU, for the field and greenhouse datasets are provided in Tables S1 and S2, respectively.

Statistical analyses

Due to differences in the total sequence reads per sample, we rarefied the field and greenhouse matrices to 7500 and 500 sequences per sample, respectively. (This eliminated one sample for the field dataset and five from the greenhouse dataset.) For the field sampling, the four sites were grouped by three ecological categories: age (45 vs. 150 year olds, hereafter referred to as younger vs. mature), habitat (fen vs. bog), or host (*Larix* vs. *Picea* vs. *Ledum*) (Table S3). To examine the effects of each of these factors on mycorrhizal fungal OTU richness and relative abundance, we conducted a series of *t* tests and ANOVAs, with mycorrhizal type (i.e., ECM, ERM, ERM-ECM) analyzed separately. Prior to running the statistical tests, variances were checked and transformed to meet assumptions of homogeneity. To examine the effects of age, habitat, and host on mycorrhizal fungal community structure by type, we used two related analyses. The first was a permutational multivariate analysis of variance (PERMANOVA) using the *adonis* function in the "vegan" package in R (R Core Team 2014; Okansanen et al. 2016). The data were first converted into Bray-Curtis dissimilarity matrices following Hellinger transformations and then run in individual models that included all three main effects (i.e., age, habitat, and host) set at 999 permutations. Due to lack of adequate replication, we did not include any interaction terms. We next applied the *betadisper* function in vegan, which assesses the degree to which the significant PERMANOVA results are determined by differences in multivariate centroid location or dispersion. Visualizations corresponding to these analyses were generated using the *metaMDS* function in vegan. To examine the relative importance of age, habitat, and host on the community structure of the dominant three mycorrhizal types (ECM, ERM, or ERM-ECM), we used the *varpart* function in vegan. We then used the *indispecies* function in vegan to determine which mycorrhizal species (based on the taxonomy assigned to the OTUs) were significantly associated with each ecological grouping variable (i.e., age, habitat, and host). We repeated the same sets of analyses for the greenhouse bioassay dataset, using host and host presence as the grouping variables. For the former, this meant analyzing the ECM, ERM, or ERM-ECM fungal communities present on a specific host, whereas for the latter we analyzed the entire ECM, ERM, or ERM-ECM mycorrhizal community present in samples when a particular host was present or absent.

Results

Following quality filtering, 387 mycorrhizal OTUs delineated from 3,303,370 sequences in the field study. Of these, 322 OTUs were included when all samples were rarefied to a depth of 7500 sequences/sample. The majority of the OTUs were ECM, although the most frequently encountered fungus was an ERM-ECM OTU (*Helotiales* sp. SH205746.07FU) and the most abundant was an ERM OTU (*Meliniomyces* sp. SH181110.07FU) (Fig. 1). Arbuscular mycorrhizal (AM)

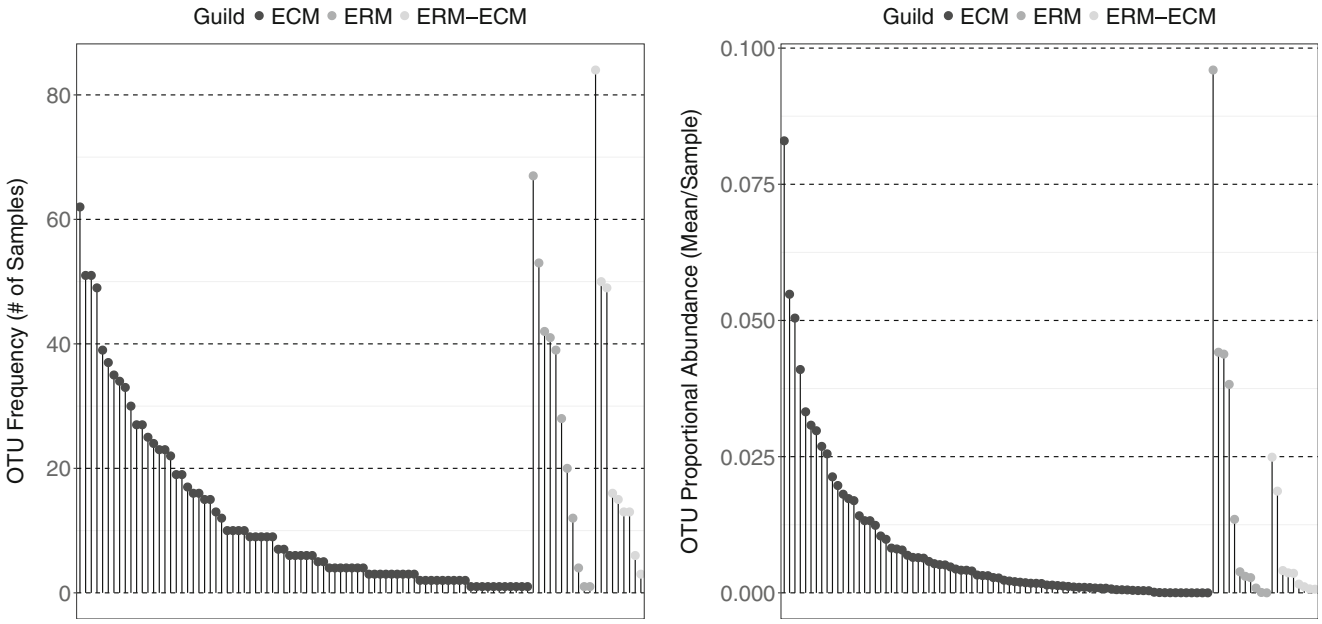

Fig. 1 Ranked Cleveland plots of mycorrhizal fungal OTU frequency and mean proportional abundance (a.k.a. relative abundance) for the field sampling at Marcell Experiment Forest. The 100 most abundant OTUs (based on rarefied sequence read counts) are plotted (from 322 total). Each line represents a single OTU, with the circle color representing its mycorrhizal guild type (*ECM* ectomycorrhizal, *ERM* ericoid, *ERM-ECM* ericoid-ectomycorrhizal). Because of their very low frequency and abundance, AM fungi are not among the top 100 mycorrhizal fungal OTUs in either plot

fungi were also present, with 12 OTUs total, but their relative abundance was extremely low (mean relative abundance/sample = < 0.0001%). As such, no further analyses were conducted on AM fungi.

The richness and abundance of the different mycorrhizal types varied by forest age, habitat, and host (Table 1(A)). OTU richness was significantly lower in young than mature forests for ERM fungi, but not significantly different for ECM or ERM-ECM fungi. Between bog and fen habitats, OTU richness was significantly lower for both ERM and ERM-ECM fungi in the fen, but not significantly different for ECM fungi. Between bog and fen habitats, OTU richness was significantly lower for both ERM and ERM-ECM fungi in the fen, but equivalent for ECM fungi. Across hosts, there was significantly greater OTU richness for ERM fungi on *Ledum* than either *Picea* or *Larix* and significantly greater OTU richness for ERM-ECM fungi on *Larix* than *Picea*, but no significance among hosts for ECM fungi. None of the mycorrhizal types varied significantly in relative abundance by either age or habitat, but ECM fungal relative abundance was significantly higher on both *Larix* and *Picea* than *Ledum*, while ERM fungal relative abundance was significantly higher on *Ledum* than *Larix* and *Picea* (Table 1(A)). There was also significantly greater relative abundance of ERM-ECM fungi on *Picea* than *Larix*.

Forest age, habitat, and host also significantly influenced the composition and dispersion of all three mycorrhizal types (Fig. 2), with each of three predictor variables being significant in all of the PERMANOVA models (Table 2(a)). Between mature and young forests, there were significant differences in community dispersion for ECM fungi, but not for ERM or ERM-ECM fungi (Table 2(a)). By habitat, community dispersion was significant for both ECM and ERM fungi, but not for ERM-ECM fungi. Across all three mycorrhizal types, there were also significant differences in community dispersion by host. The amount of variation in community composition explained by age, habitat, and host varied among mycorrhizal types (Fig. 3). For ERM and ERM-ECM fungal communities, host explained at least twice the amount of variation as either age or habitat and, cumulatively, these three variables explained between 27 and 32% of the variation. In contrast, for ECM fungal communities, habitat accounted for the largest amount of variation in community composition, although the total amount of variation explained by these three variables was lower relative to other guilds (18%).

Many mycorrhizal fungal species were significantly associated with specific forest ages, habitats, and hosts (Table 3). *Larix* hosted the greatest number of indicator species (24), followed by *Ledum* (7) and *Picea* (6). Many *Larix*-associated species included known ECM fungal specialists in the genus *Suillus*, although two ERM-ECM species were also part of this group. Members of the ECM genus *Cortinarius* formed significant associations with *Picea*, while on *Ledum*, the significant associations primarily involved Sebacinalean ERM fungi. Because the fen was dominated *Larix* (i.e., it had only two *Ledum* and no *Picea* samples), many of the association patterns for the fen tracked those of *Larix*. By age, patterns of

Table 1 Summary of mycorrhizal fungal OTU richness and relative abundance by (A) age, habitat, and host in the field sampling and by (B) host and host presence in the greenhouse sampling

A. Field sampling									
Mycorrhizal type	Variable	Age		Habitat		Host			
		Mature	Young	Bog	Fen	*Larix*	*Ledum*	*Picea*	
	Sample size	50	40	79	11	28	32	30	
ECM	OTU richness (number observed)	16 (5) a	15 (7) a	15 (5) a	19 (8) a	17 (7) a	15 (5) a	16 (4) a	
	Relative abundance (sum/sample)	0.66 (0.32) a	0.73 (0.33) a	0.67 (0.32) a	0.82 (0.34) a	0.95 (0.03) a	0.34 (0.26) b	0.83 (0.17) a	
ERM	OTU richness (number observed)	5 (3) a	4 (2) b	5 (2) a	2 (2) b	2 (2) b	6 (2) a	4 (2) a	
	Relative abundance (sum/sample)	0.28 (0.32) a	0.20 (0.31) a	0.26 (0.32) a	0.12 (0.29) a	0.01 (0.02) b	0.60 (0.25) a	0.09 (0.14) b	
ERM-ECM	OTU richness (number observed)	4 (2) a	4 (1) a	4 (1) a	2 (1) b	4 (2) a	4 (2) ab	3 (1) b	
	Relative abundance (sum/sample)	0.06 (0.08) a	0.06 (0.07) a	0.06 (0.07) a	0.06 (0.09) a	0.03 (0.02) b	0.06 (0.08) ab	0.08 (0.10) b	
B. Greenhouse bioassay									
Mycorrhizal type	Variable	Host			*Ledum* present		*Larix* present		*Picea* present	
		Larix	Ledum	Picea	No	Yes	No	Yes	No	Yes
ECM	Sample size	16	14	14	17	27	17	27	17	27
	OTU richness (number observed)	5 (2) a	6 (3) a	6 (2) a	6 (2) a	5 (2) a	5 (2) a	6 (2) a	5 (2) a	6 (2) a
	Relative abundance (sum/sample)	0.98 (0.03)	0.45 (0.43)	0.82 (0.33)	0.99 (< 0.01)	0.61 (0.42)	0.57 (0.45)	0.89 (0.25)	0.6 (0.45)	0.87 (0.28)
ERM	OTU richness (number observed)	1 (1) b	3 (2) a	1 (1) a	< 1 (1) b	3 (2) a	2 (2) a	2 (2) a	3 (2) a	1 (2) a
	Relative abundance (sum/sample)	0.02 (0.03)	0.53 (0.41)	0.17 (0.33)	< 0.01 (< 0.01)	0.37 (0.4)	0.41 (0.43)	0.11 (0.25)	0.38 (0.42)	0.13 (0.28)
ERM-ECM	OTU richness (number observed)	< 1 (1) a	1 (2) a	< 1 (1) a	< 1 (1) a	0.8 (1) a	1 (2) a	< 1 (1) a	1 (2) a	< 1 (1) a
	Relative abundance (sum/sample)	< 0.01 (< 0.01) a	0.02 (0.04) a	< 0.01 (< 0.01) a	< 0.01 (< 0.01) a	0.01 (0.03) a	0.02 (0.04) a	< 0.01 (< 0.01) a	0.02 (0.04) a	< 0.01 (< 0.01) a

Values represent mean (± 1 SD). Different letters indicate significant differences within each ecological factor and mycorrhizal type

ECM ectomycorrhizal, *ERM* ericoid, *ERM-ECM* ericoid-ectomycorrhizal

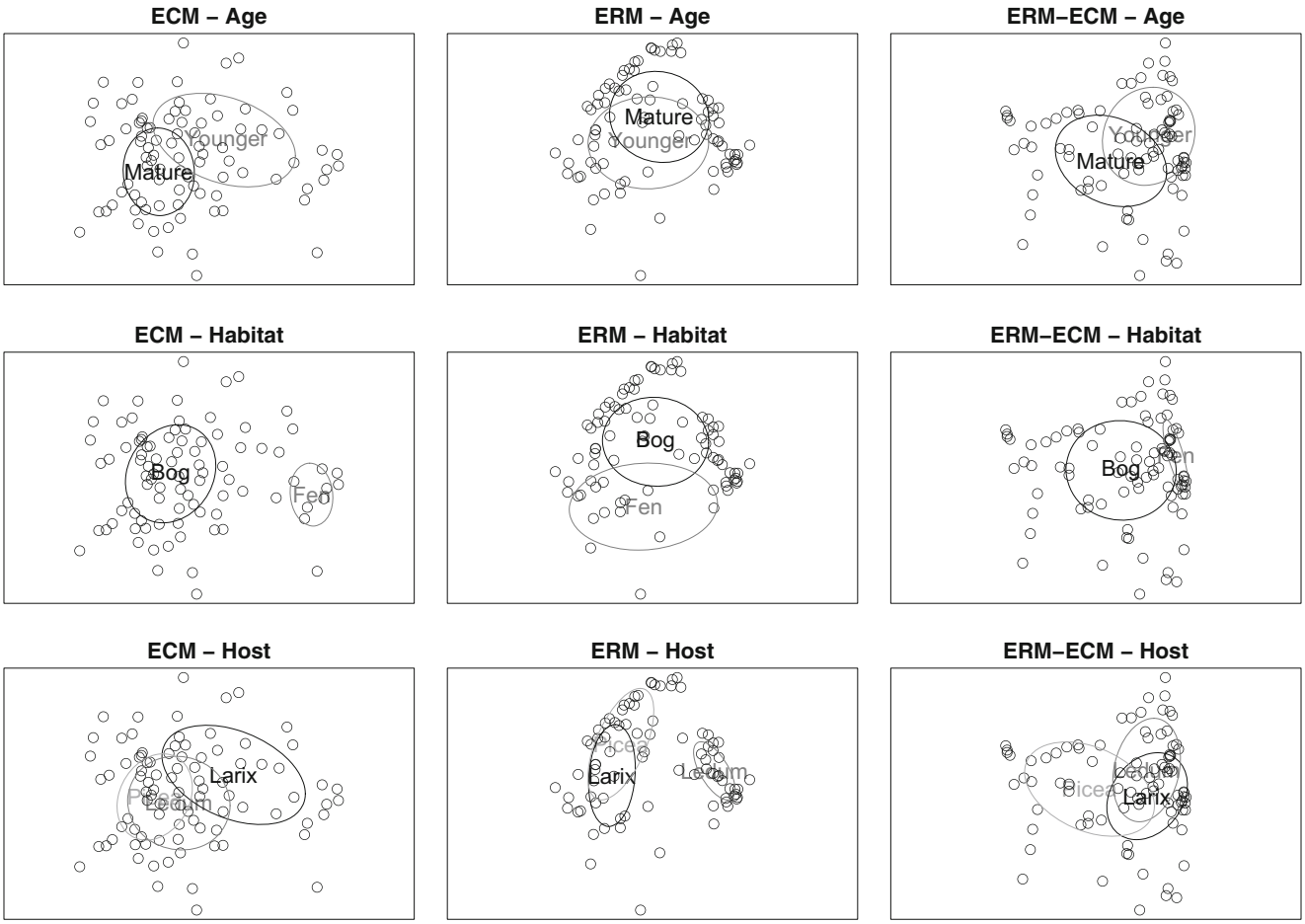

Fig. 2 Non-metric multidimensional scaling plots of mycorrhizal fungal community composition by age (younger v. mature), habitat (fen v. bog), and host (*Larix* vs. *Ledum* vs. *Picea*) in the field sampling. Circles represent standard deviation ellipses to better visualize community dispersion. *ECM* ectomycorrhizal, *ERM* ericoid, *ERM-ECM* ericoid-ectomycorrhizal

association were dominated by differences in ECM fungi, with the young forests having many significant associations with *Suillus* and *Lactarius* species and the old forests associating with *Cortinarius* and *Craterellus* species.

In the greenhouse bioassay, there were a total of 147 OTUs delineated from the 1,573,539 sequences that passed quality filtering. A total of 41 OTUs remained after samples were rarefied to a depth of 500 sequences/sample. OTU richness varied depending on host species as well as host presence across the three dominant mycorrhizal types (Table 1(B)). By host species, OTU richness of ERM fungi was significantly higher on *Ledum* than *Larix* and *Picea* but did not vary significantly for either ECM or ERM-ECM fungi. Similarly, when grouped by host presence, OTU richness significantly increased when *Ledum* was present for ERM fungi, but not for ECM or ERM-ECM fungi. The presence of *Larix* did not significantly influence the OTU richness for any mycorrhizal type, while the presence of *Picea* significantly decreased the OTU richness for ERM fungi. As in the field study, OTU relative abundance tracked known host associations, with ECM fungi having significantly higher abundance on *Larix* and *Picea* than *Ledum* and ERM fungi having significantly higher abundance of *Ledum* than *Larix* or *Picea*. For ERM-ECM fungi, there was also a significantly greater abundance on *Ledum* than *Larix* (Table 1(B)).

Host and host presence also influenced mycorrhizal fungal community composition in the greenhouse bioassay (Fig. S3; Fig. 4, respectively). In the PERMANOVA models, host was a significant predictor of composition for all three mycorrhizal types (Table 2(b)). Similarly, the presence of *Ledum* significantly affected community composition for all three mycorrhizal types. The presence of *Larix* and *Picea*, however, had lesser effects, with only ECM fungal community composition being influenced significantly by *Larix* presence. In all cases, community dispersion was not significantly different by host. In contrast, *Larix* presence only significantly influenced ECM community composition and *Picea* presence had no significant effects.

Discussion

Both ECM and ERM fungi have long been recognized to play a major role in plant nutrient acquisition in highly organic

Table 2 Summary of adonis and betadisper analyses of the effects of age, habitat, and host on mycorrhizal fungal community composition in the (a) field sampling and (b) greenhouse bioassay

A.	Age	Habitat	Host	
Adonis				
ECM	***	***	***	
ERM	**	***	*	
ERM-ECM	***	***	***	
Betadisper				
ECM	***	***	***	
ERM	ns	ns	**	
ERM-ECM	ns	ns	*	
B.	Host	*Ledum* present	*Larix* present	*Picea* present
Adonis				
ECM	***	*	***	ns
ERM	***	***	ns	ns
ERM-ECM	*	*	ns	ns
Betadisper				
ECM	ns	*	**	*
ERM	ns	***	na	na
ERM-ECM	ns	ns	na	na

ns not sig, *na* not attempted, *ECM* ectomycorrhizal, *ERM* ericoid, *ERM-ECM* ericoid-ectomycorrhizal.

*< 0.05; **< 0.01; ***< 0.001 significance codes

soils, including those found in peatland forests (Read and Perez-Moreno 2003). In many forests, particularly at higher latitudes, both host types frequently co-occur (Read 1991). What has been less clear to date is how these functionally similar mycorrhizal types respond to shared ecological niche axes. The results of our study suggest that despite notable overlap in host distributions, the ECM and ERM fungal communities in peatland forests respond differently to forest age, habitat, and host species.

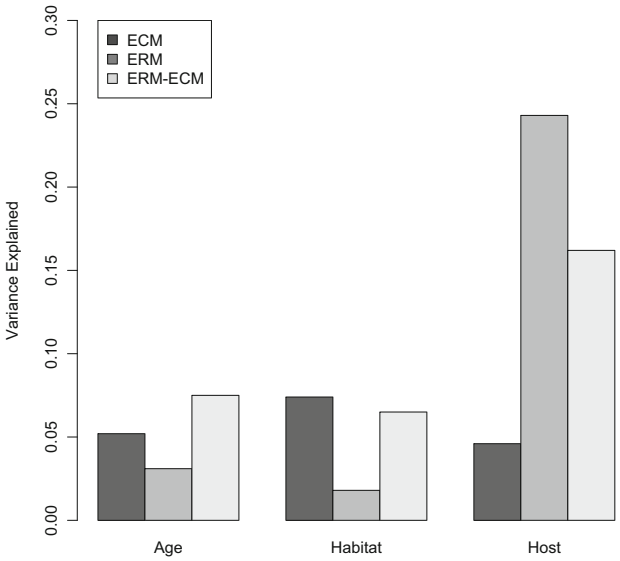

Fig. 3 Amount of variance in community composition of the three dominant mycorrhizal types explained by age, habitat, and host in the field sampling. Values represent the adjusted R^2 values for each factor when controlling the effects of the other two factors based on variance partitioning analyses. *ECM* ectomycorrhizal, *ERM* ericoid, *ERM-ECM* ericoid-ectomycorrhizal

The strong effects of host species are not surprising given the known affiliations of ECM and ERM fungi for the hosts sampled. That said, the contrasting patterns of OTU richness and relative abundance by host revealed interesting differences in the association capacities of ECM and ERM fungi. In both the field sampling and the greenhouse bioassay, ECM fungal OTU richness on *Ledum* (a known ericaceous host) was largely equivalent to that on *Larix* and *Picea* (known ectomycorrhizal hosts). These results are consistent with other studies demonstrating that ericaceous hosts can host ECM fungi, particularly *Arbutus* and *Arctostaphylos* species, which form ecto-endomycorrhizas with many ECM fungi (Molina and Trappe 1982; Horton et al. 1999; Kennedy et al. 2012). Relatively high ECM fungal richness has also been noted on ericaceous shrubs in US forests (Dighton and Coleman 1992; Smith et al. 1995) and arctic habitats (Lorberau et al. 2017). In contrast to the OTU richness patterns we observed, however, the notably low relative abundance of ECM fungi on *Ledum* compared to *Larix* and *Picea* (Read 1991; Serreze et al. 2000; Read et al. 2004; Wieder and Vitt 2006; Kolka et al. 2011) suggests that these ECM associations were limited in extent. Others have similarly found that ECM fungi can weakly colonize non-traditional hosts (Duddridge 1986; Smith et al. 1995), possibly due to greater carbon access from overstory hosts (Hogberg et al. 1999). It should also be noted that without observing Hartig nets, the limited colonization patterns could just reflect surface level colonization of alternative hosts rather than functional ectomycorrhizas. In contrast to ECM fungi, the patterns for ERM fungi were narrower in terms of host association. Specifically, both OTU richness and relative abundance were high only on *Ledum*. Understanding why these ERM fungi are less able to colonize ECM hosts is an important direction of future research, as a number of related fungi are able to successfully associate with both types of hosts (i.e., ERM-ECM fungi).

With regard to habitat, differential host abundance (i.e., the absence of *Picea* and very limited *Ledum* presence in the fen) could, in part, explain the overall differences in ECM, ERM, and ERM-ECM fungal OTU richness and community composition. However, when only the mycorrhizal communities on *Larix* in young forests were compared, there were still significant differences in OTU richness for all three types of mycorrhizal fungi. ECM fungal OTU richness more than doubled in the fen, whereas the ERM and ERM-ECM fungal OTU richness dropped by more than half (Fig. S4). These differences are likely associated with significant changes in abiotic factors between fens and bogs (e.g., pH and nutrient availability; Glaser 1987), which are known to affect the

Table 3 Indicator species analysis of the three dominant mycorrhizal types by age, habitat, and host

Age		Habitat			Host		
Younger	Mature	Fen		Bog	*Larix*	*Picea*	*Ledum*
ECM fungi							
Hebeloma sp. (SH218907)	*Agaricomycetes* sp. (SH202674)	*Cortinarius hemitrichus* (SH197819)	*Thelephora terrestris* (SH184510)	*Ascomycota* sp. (SH214267)	*Endogone* sp. (SH213348)**	*Acephala applanata* (SH275913)	*Acephala* sp. (SH204998)
Lactarius glyciosmus (SH227199)	*Cortinarius* sp. (SH188561)	*Endogone* sp. (SH213348)	*Thelephoraceae* sp. (SH185274)	*Cortinarius biformis* (SH188479)	*Hebeloma* sp. (SH218907)	*Cortinarius casimiri* (SH188471)	
Lactarius helvus (SH214492)	*Cortinarius casimiri* (SH188471)**	*Geopora* sp. (SH213677)	*Thelephoraceae* sp. (SH189432)	*Cortinarius brunneus* (SH264910)	*Inocybaceae* sp. (SH176524)	*Cortinarius tillamookensis* (SH135196)	
Piloderma sp. (SH196707)	*Cortinarius malachius* (SH188502)	*Hebeloma asperulatum* (SH293510)	*Tomentella coerulea* (SH177784)	*Cortinarius casimiri* (SH188471)	*Inocybe lacera* (SH201233)	*Hebeloma incarnatulum* (SH215995)	
Russula sp. (SH176559)	*Craterellus tubaeformis* (SH216284)***	*Hebeloma* sp. (SH218907)	*Tomentella ellisii* (SH189370)	*Hebeloma incarnatulum* (SH215995)	*Laccaria laccata* (SH220988)	*Oidiodendron pilicola* (SH216991)	
Russula versicolor (SH219856)	*Hebeloma incarnatulum* (SH215995)	*Inocybaceae* sp. (SH176524)	*Tomentella ellisii* (SH189381)**	*Lactarius* sp. (SH182395)	*Piloderma* sp. (SH196707)		
Sebacinales sp. (SH179999)	*Laccaria laccata* (SH220988)	*Inocybe lacera* (SH201233)	*Tomentella* sp. (SH177803)	*Meliniomyces* sp. (SH181110)	*Russula versicolor* (SH219856)		
Suillus elbensis (SH176748)	*Russula decolorans* (SH176548)	*Inocybe* sp. (SH201236)	*Tomentella* sp. (SH177906)	*Piloderma sphaero sporum* (SH196824)	*Sebacinales* sp. (SH179999)		
Suillus grevillei (SH176747)	*Thelephoraceae* sp. (SH189432)	*Inocybe substraminipes* (SH283266)	*Tomentella* sp. (SH189367)	*Sebacinales* sp. (SH197469)	*Suillus ampliporus* (SH176762)		
Suillus paluster (SH176767)		*Laccaria laccata* (SH220988)	*Tomentella* sp. (SH527169)**	*Thelephoraceae* sp. (SH189432)	*Suillus grevillei* (SH176747)		
Suillus spectabilis (SH176766)		*Lactarius glyciosmus* (SH227199)	*Tuber* sp. (SH188859)		*Suillus paluster* (SH176767)		
Tomentella coerulea (SH177784)		*Leotiomycetes* sp. (SH181092)	*Wilcoxina mikolae* (SH194156)		*Suillus spectabilis* (SH176766)		
Tomentella ellisii (SH189381)		*Peziza badia* (SH193723)			*Suillus elbensis* (SH176748)		
Tomentella sublilacina (SH184509)		*Piloderma* sp. (SH196707)			*Thelephoraceae* sp. (SH185274)		
Tomentellopsis submollis (SH184844)		*Russula versicolor* (SH219856)			*Tomentella coerulea* (SH177784)		
Tuber sp. (SH188859)		*Sebacinales* sp. (SH179999)			*Tomentella ellisii* (SH189381)		
		Suillus spectabilis (SH176766)			*Tomentella* sp. (SH189367)		
		Suillus grevillei (SH176747)			*Tomentella* sp. (SH527169)		
		Suillus subaureus (SH079593)			*Tuber* sp. (SH188859)		

Table 3 (continued)

Age		Habitat		Host		
Younger	Mature	Fen	Bog	*Larix*	*Picea*	*Ledum*
		Suillus elbensis (SH176748)		*Wilcoxina mikolae* (SH194156)		
ERM fungi						
	Sebacinales sp. (SH179096)					*Helotiales* sp. (SH205746)
	Oidiodendron sp. (SH216996)					*Oidiodendron maius* (SH216987)
						Sebacinales sp. (SH179096)**
						Sebacinales (SH180013)
						Sebacinales sp.(SH197469)
ERM-ECM fungi						
Rhizoscyphus sp. (SH214292)	*Meliniomyces* sp. (SH181110)	*Meliniomyces* sp. (SH181080)		*Rhizoscyphus* sp. (SH214292)	*Meliniomyces* sp. (SH181110)	
Meliniomyces sp. (SH181080)				*Meliniomyces* sp. (SH181080)		
Rhizoscyphus sp. (SH214292)						

Multiple OTUs matched the same SH record. Number of asterisks equals the number of matches

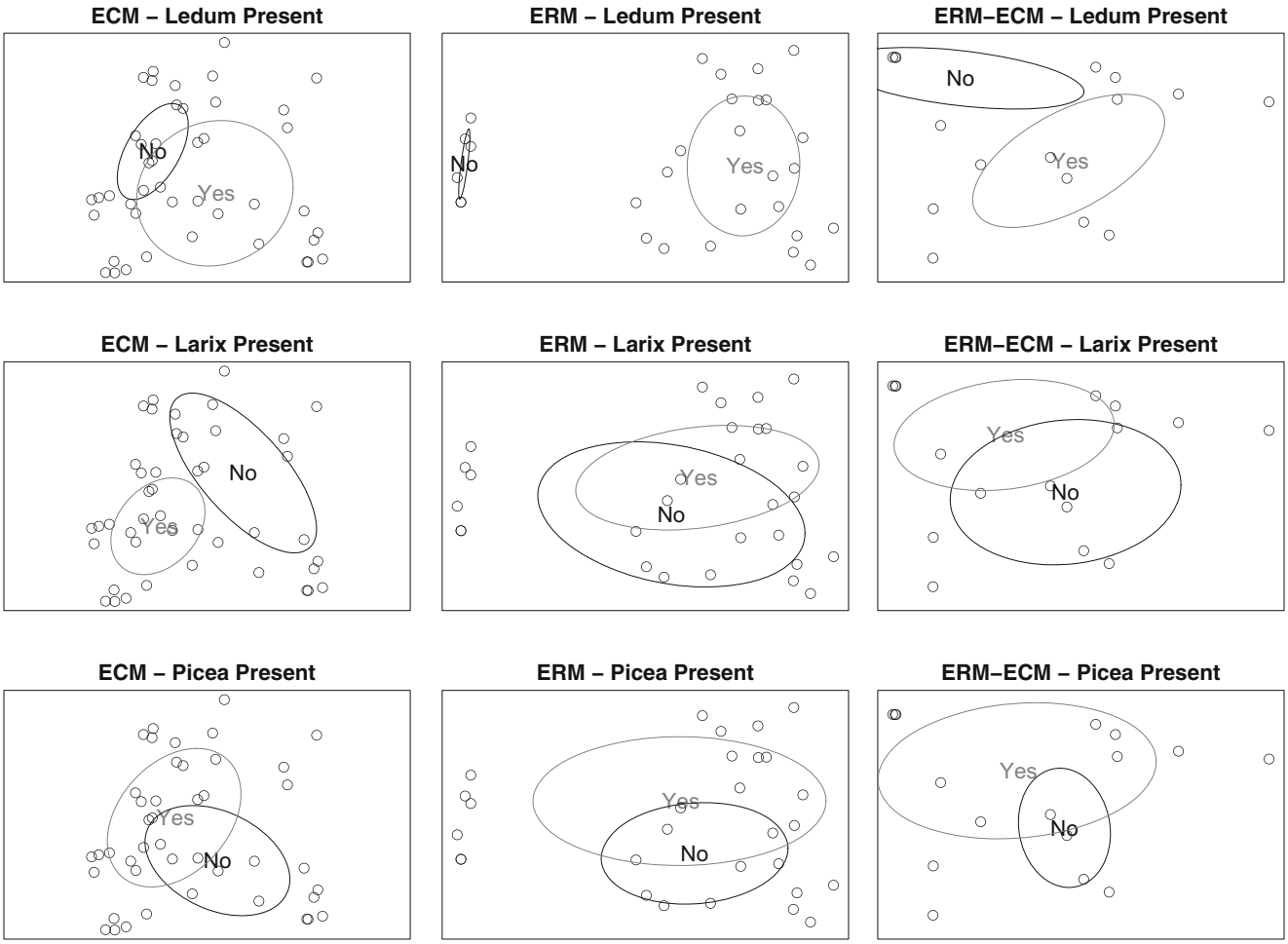

Fig. 4 Non-metric multidimensional scaling plots of mycorrhizal fungal community composition by host presence in the greenhouse bioassay. Circles represent standard deviation ellipses to better visualize community dispersion. ECM ectomycorrhizal, ERM ericoid, ERM-ECM ericoid-ectomycorrhizal

richness and abundance of both mycorrhizal types (Wurzburger et al. 2011; Suz et al. 2014). Similarly, the effect of forest age was also still significant when comparing only the younger and mature sites in which all hosts were present (S1 vs. S6; Fig. S5). Although a significant increase in ECM fungal OTU richness in mature forests does match with some other studies (Vasser et al. 1995; Twieg et al. 2007), how forest age affects ERM fungal OTU richness is less well understood. Dickie et al. (2013) suggested ERM diversity may increase rather than decline with forest age, due to the buildup of organic matter. Regardless of the specific mechanisms driving these differences, our additional analyses, while limited in site replication, further support the overall results that different mycorrhizal types vary in their responses to shared ecological niche axes.

Forest age, habitat, and host also differentially influenced mycorrhizal community structure. This effect for both ECM and ERM fungi appeared to be largely a combination of differences in composition (i.e., location of grouping variable centroids in multi-dimensional space) as well as dispersion (i.e., spread around each grouping variable in multi-dimensional space) for all three factors. For age, we observed that community dispersion was typically greater in the younger forests, which may reflect increasing abiotic filtering effects as bogs age (i.e., increasing acidity and correspondingly lower nutrient availability; Heinselsman 1970). For habitat, ECM fungal OTU richness was much higher in the fen, but community dispersion was much lower. We speculate that this may be due to the fact that the bogs contain both *Larix* and *Picea* hosts, while fens only contained *Larix*. This may lower root competition in the fen, which could increase ECM species richness, while at the same time selecting for a more uniform community, including a number of *Larix* ECM specialists. Finally, there were also differences in mycorrhizal community composition and dispersion by host. As with habitat, we believe that the higher dispersion on *Larix* for ECM fungi likely reflects host occurrence in both fens and bogs, while the tight constraint on ERM fungal communities on *Ledum* could reflect a combination of relatively low overall OTU richness and a particularly high abundance of a single ERM OTU.

Our redundancy analysis, which we used to assess the relative importance of age, habitat, and host as

factors influencing mycorrhizal community structure, was largely consistent with current knowledge about both ECM and ERM fungal communities. In particular, previous studies have found that there is often considerable overlap in the ECM fungal communities of co-occurring conifers (Horton and Bruns 1998; Cullings et al. 2000; Horton et al. 2005). This likely explains why habitat had a greater effect, despite both *Larix* and *Picea* had some ECM taxa that exhibited notable host preference. With regard to patterns of host specificity, members of the ECM fungal genus *Suillus*, which are considered *Larix* specialists in this system, did have sequence reads in both *Ledum* and *Picea* host samples. The read counts on these two alternative hosts, however, were significantly lower than in *Larix* samples in the field study and they were functionally absent from the S2 site (where *Larix* was naturally absent) as well as when *Larix* seedlings were absent in the greenhouse bioassay (Table S4). Collectively, this suggests that *Picea* is only likely to be a host of *Suillus* ECM fungi in forests where other conifer hosts (*Larix*, *Pseudotsuga*, or *Pinus*) are also present (Wurzburger et al. 2004; Nguyen et al. 2016). For ERM fungi, the strong host effect we observed is inconsistent with the current literature for this mycorrhizal type, which suggests that host specificity among ERM hosts is low (Leopold 2016). Instead, as noted above, our result is likely due to the limited compatibility between these fungi and ECM hosts.

The results of the greenhouse bioassay largely mirrored the field sampling in terms of the trends in OTU richness and relative abundance for all three mycorrhizal types. This suggests that even though the seedlings had some prior mycorrhizal colonization and the experiment lasted only 7 months, the results we obtained captured realistic ecological dynamics. Interestingly, the presence of *Ledum* had much stronger effects of mycorrhizal community composition than either *Larix* or *Picea*. We speculate that this may be due to the older age of the *Ledum* individuals, which had root systems that were approximately twice as large as the conifers at the beginning of the experiment. Previous work has shown that while ericaceous shrubs can inhibit the growth of ECM hosts (Mallik 2003), some mycorrhizal fungi have the ability to counteract the allelopathic effects of *Kalmia* and *Ledum* plants. In our study, we found that two ECM taxa in the genus *Suillus* (*S. elbensis* and *S. ampliporus*) and four in the order Sebacinales (group B) were significantly associated with *Ledum* presence (Table S5). Since none of these taxa have been tested in prior mycorrhizal-mediated allelopathy assays, the *Suillus* species, in particular (which readily colonize seedlings via spore inoculation), may represent promising new species for nursery inoculations to facilitate conifer re-establishment in areas currently dominated by ericaceous shrubs.

Conclusions

Given the disproportionate effects of climate warming at high latitudes, the mycorrhizal fungal communities in boreal peatland forests are currently experiencing significant changes in environmental conditions. Our study provides an important characterization of these mycorrhizal fungal communities and explores the relative effects of different ecological niche axes. Large-scale experiments such as SPRUCE (Hanson et al. 2012) have been initiated to better understand the effects of increased warming and higher carbon dioxide concentrations. We believe that mycorrhizal fungi will likely play an important role in peatland forest responses, both as symbionts aiding plant nutrient acquisition as well as effectors of decomposition dynamics (Read et al. 2004; Fernandez and Kennedy 2016). In particular, our results suggest that paying specific attention to different mycorrhizal types is important, as their responses are not likely to be uniform. Future studies examining finer-scale intervals across these ecological niche axes as well as possible interactions among different ecological factors will be important in better identifying the specific environmental conditions that structure belowground community dynamics of peatland forest ecosystems.

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References

Asemaninejad A, Thorn RG, Lindo Z (2017) Vertical distribution of fungi in hummocks and hollows of boreal peatlands. Fungal Ecol 27:59–68. https://doi.org/10.1016/j.funeco.2017.02.002

Bogar LM, Kennedy PG (2013) New wrinkles in an old paradigm: neighborhood effects can modify the structure and specificity of Alnus-associated ectomycorrhizal fungal communities. FEMS Microbiol Ecol 83(3):767–777. https://doi.org/10.1111/1574-6941.12032

Clemmensen KE, Michelsen A, Jonasson S, Shaver GR (2006) Increased ectomycorrhizal fungal abundance after long-term fertilization and warming of two arctic tundra ecosystems. New Phytol 171:391–404

Collier LCS, Mallik AU (2010) Does post-fire abiotic habitat filtering create divergent plant communities in black spruce forests of eastern Canada? Oecologia 164(2):465–477. https://doi.org/10.1007/s00442-010-1642-0

Cullings KW, Vogler DR, Parker VT, Finley SK (2000) Ectomycorrhizal specificity patterns in a mixed Pinus contorta and Picea engelmannii forest in Yellowstone National Park. Appl Environ Microbiol 66(11):4988–4991. https://doi.org/10.1128/AEM.66.11.4988-4991.2000

Deslippe JR, Hartmann M, Mohn WW, Simard SW (2011) Long-term experimental manipulation of climate alters the ectomycorrhizal

community of Betula nana in Artic tundra. Glob Chang Biol 17(4): 1625–1636. https://doi.org/10.1111/j.1365-2486.2010.02318.x

Dickie IA, Martinez-Garcia LB, Koele N et al (2013) Mycorrhizas and mycorrhizal fungal communities throughout ecosystem development. Plant Soil 367(1-2):11–39. https://doi.org/10.1007/s11104-013-1609-0

Dighton J, Coleman DC (1992) Phosphorus relations of roots and mycorrhizas of Rhododendron maximum L. in the southern Appalachians, North Carolina. Mycorrhiza 1:175–184

Duddridge JA (1986) The development and ultrastructure of ectomycorrhizas. IV. Compatible and incompatible interactions between Suillus grevillei (Klotzcsh) Sing. and a number of ectomycorrhizal hosts in vitro in the presence of exogenous carbohydrate. New Phytol 103(3):465–471. https://doi.org/10.1111/j.1469-8137.1986.tb02884.x

Fernandez CW, Kennedy PG (2016) Revisiting the 'Gadgil effect': do interguild fungal interactions control carbon cycling in forest soils ? New Phytol 209(4):1382–1394. https://doi.org/10.1111/nph.13648

Fernandez CW, Nguyen NH, Stefanski A, Han Y, Hobbie SE, Montgomery RA, Reich PB, Kennedy PG (2017) Ectomycorrhizal fungal response to warming is linked to poor host performance at the boreal-temperate ecotone. Glob Chang Biol 23(4):1598–1609. https://doi.org/10.1111/gcb.13510

Glaser P (1987) The ecology of patterned boreal peatlands of northern Minneosta: a community profile. U.S. Fish Wildl Serv report 85-7. 98 pp

Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol Appl 1(2):182–195. https://doi.org/10.2307/1941811

Hanson P, Riggs JS, Nettles WR et al (2012) Attaining whole-ecosystem warming using air and deep-soil heating methods with an elevated CO2 atmosphere. Biogeosciences 14:861–883

Hanson PJ, Riggs JS, Nettles WR, Phillips JR, Krassovski MB, Hook LA, Gu L, Richardson AD, Aubrecht DM, Ricciuto DM, Warren JM (2017) Attaining whole-ecosystem warming using air and deep-soil heating methods with an elevated CO 2 atmosphere. Biogeosciences 14:861–883

Heinselsman ML (1970) Landscape evolution, peatland types, and the environment in the Lake Agassiz peatlands natural area, Minnesota. Ecol Monogr 40(2):235–261. https://doi.org/10.2307/1942297

Hiiesalu I, Bahram M, Tdersoo L (2017) Plant species richness and productivity determine the diversity of soil fungal guilds in temperate coniferous forest and bog habitats. Mol Ecol 26(18):4846–4858. https://doi.org/10.1111/mec.14246

Hogberg P, Plamboeck AH, Taylor AFS, Fransson PMA (1999) Natural 13C abundance reveals trophic status of fungi and host-origin of carbon in mycorrhizal fungi in mixed forests. PNAS 96(15):8534–8539. https://doi.org/10.1073/pnas.96.15.8534

Horton TR, Bruns TD (1998) Multiple-host fungi are the most frequent and abundant ectomycorrhizal types in a mixed stand of Douglas fir (Pseudotsuga menziesii) and bishop pine (Pinus muricata). New Phytol 139(2):331–339. https://doi.org/10.1046/j.1469-8137.1998.00185.x

Horton TR, Bruns TD, Parker VT (1999) Ectomycorrhizal fungi associated with Arctostaphylos contribute to Pseudotsuga menziesii establishment. Can J Bot Can Bot 77:93–102

Horton TR, Molina RJ, Hood K (2005) Douglas-fir ectomycorrhizae in 40- and 400-year-old stands: mycobiont availability to late successional western hemlock. Mycorrhiza 15(6):393–403. https://doi.org/10.1007/s00572-004-0339-9

Johnstone JF, Chapin FS (2006) Effects of soil burn severity on post-fire tree recruitment in boreal forest. Ecosystems 9(1):14–31. https://doi.org/10.1007/s10021-004-0042-x

Kennedy PG, Izzo AD, Bruns TD (2003) There is high potential for the formation of common mycorrhizal networks between understorey and canopy trees in a mixed evergreen forest. J Ecol 91(6):1071–1080. https://doi.org/10.1046/j.1365-2745.2003.00829.x

Kennedy PG, Smith DP, Horton TR, Molina RJ (2012) Arbutus menziesii (Ericaceae) facilitates regeneration dynamics in mixed evergreen forests by promoting mycorrhizal fungal diversity and host connectivity. Am J Bot 99:1691–701

Kõljalg U, Nilsson RH, Abarenkov K, Tedersoo L, Taylor AFS, Bahram M, Bates ST, Bruns TD, Bengtsson-Palme J, Callaghan TM, Douglas B, Drenkhan T, Eberhardt U, Dueñas M, Grebenc T, Griffith GW, Hartmann M, Kirk PM, Kohout P, Larsson E, Lindahl BD, Lücking R, Martín MP, Matheny PB, Nguyen NH, Niskanen T, Oja J, Peay KG, Peintner U, Peterson M, Põldmaa K, Saag L, Saar I, Schüßler A, Scott JA, Senés C, Smith ME, Suija A, Taylor DL, Telleria MT, Weiss M, Larsson KH (2013) Towards a unified paradigm for sequence-based identification of fungi. Mol Ecol 22(21):5271–5277. https://doi.org/10.1111/mec.12481

Kolka R, Sebesyten S, Verry ES et al (2011) Peatland biogeochemistry and watershed hydrology at the Marcell Experimental Forest. CRC Press, Boca Raton

Leopold DR (2016) Ericoid fungal diversity: challenges and opportunities for mycorrhizal research. Fungal Ecol 24:114–123. https://doi.org/10.1016/j.funeco.2016.07.004

Lindahl BD, Nilsson RH, Tedersoo L, Abarenkov K, Carlsen T, Kjøller R, Kõljalg U, Pennanen T, Rosendahl S, Stenlid J, Kauserud H (2013) Fungal community analysis by high-throughput sequencing of amplified markers—a user's guide. New Phytol 199(1):288–299. https://doi.org/10.1111/nph.12243

Lorberau KE, Botnen SS, Mundra S, Aas AB, Rozema J, Eidesen PB, Kauserud H (2017) Does warming by open-top chambers induce change in the root-associated fungal community of the arctic dwarf shrub Cassiope tetragona (Ericaceae)? Mycorrhiza 27(5):513–524. https://doi.org/10.1007/s00572-017-0767-y

Mallik AU (2003) Conifer regeneration problems in boreal and temperate forests with ericaceous understory: role of disturbance, seedbed limitation, and keytsone species change. Crit Rev Plant Sci 22(3-4): 341–366. https://doi.org/10.1080/713610860

Martin M (2011) Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet J 17:10–12

Mohan JE, Cowden CC, Baas P, Dawadi A, Frankson PT, Helmick K, Hughes E, Khan S, Lang A, Machmuller M, Taylor M, Witt CA (2014) Mycorrhizal fungi mediation of terrestrial ecosystem responses to global change: mini-review. Fungal Ecol 10:3–19. https://doi.org/10.1016/j.funeco.2014.01.005

Molina R, Trappe JM (1982) Lack of mycorrhizal specificity by the ericaceous hosts Arbutus menziesii and arctostaphylos uva-ursi. New Phytol 90(3):495–509. https://doi.org/10.1111/j.1469-8137.1982.tb04482.x

Nguyen N, Song Z, Bates S et al (2016) FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecol 20:241–248. https://doi.org/10.1016/j.funeco.2015.06.006

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens HH, Szoecs E, Wagner H (2017) vegan: Community Ecology Package. R package version 2.4-4. Available from https://CRAN.Rproject.org/package=vegan. Accessed 5 Aug 2017

Peay KG, Kennedy PG, Talbot JM (2016) Dimensions of biodiversity in the Earth mycobiome. Nat Rev Microbiol 14(7):434–447. https://doi.org/10.1038/nrmicro.2016.59

R Core Team (2014) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/. Accessed 1 Aug 2017

Read DJ (1991) Mycorrhizas in ecosystems. Exp Dermatol 47:376–391

Read DJ, Perez-Moreno J (2003) Mycorrhizas and nutrient cycling in ecosystems—a journey towards relevance? New Phytol 157(3): 475–492. https://doi.org/10.1046/j.1469-8137.2003.00704.x

Read DJ, Leake JR, Perez-Moreno J (2004) Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes 82: 1243–1263

Reich PB, Sendall KM, Rice K, Rich RL, Stefanski A, Hobbie SE, Montgomery RA (2015) Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. Nat Clim Chang 5(2):148–152. https://doi.org/10.1038/nclimate2497

Serreze MC, Walsh JE, Chapin FS III et al (2000) Observational evidence of recent change in the northern high-latitude environment. Clim Chang 46(1/2):159–207. https://doi.org/10.1023/A:1005504031923

Smith DP, Peay KG (2014) Sequence depth, not PCR replication, improves ecological inference from next generation DNA sequencing. PLoS One 9(2):e90234. https://doi.org/10.1371/journal.pone.0090234

Smith JE, Molina R, Perry DA (1995) Occurrence of ectoraycorrhizas on ericaceous and coniferous seedlings grown in soils from the Oregon coast range. New Phytol 129(1):73–81. https://doi.org/10.1111/j.1469-8137.1995.tb03011.x

Sun H, Terhonen E, Kovalchuk A, Tuovila H, Chen H, Oghenekaro AO, Heinonsalo J, Kohler A, Kasanen R, Vasander H, Asiegbu FO (2016) Dominant tree species and soil type affect the fungal community structure in a boreal peatland forest. Appl Environ Microbiol 82(9):2632–2643. https://doi.org/10.1128/AEM.03858-15

Suz LM, Barsoum N, Benham S, Dietrich HP, Fetzer KD, Fischer R, García P, Gehrman J, Kristöfel F, Manninger M, Neagu S, Nicolas M, Oldenburger J, Raspe S, Sánchez G, Schröck HW, Schubert A, Verheyen K, Verstraeten A, Bidartondo MI (2014) Environmental drivers of ectomycorrhizal communities in Europe's temperate oak forests. Mol Ecol 23(22):5628–5644. https://doi.org/10.1111/mec.12947

Tedersoo L, Sadam A, Zambrano M, Valencia R, Bahram M (2010) Low diversity and high host preference of ectomycorrhizal fungi in Western Amazonia, a neotropical biodiversity hotspot. The ISME Journal 4:465–71

Tedersoo L, Bahram M, Põlme S et al (2014) Global diversity and geography of soil fungi. Science 346:1078

Thormann MN, Rice AV (2007) Fungi from peatlands. Fungal Divers: 241–299

Twieg BD, Durall DM, Simard SW (2007) Ectomycorrhizal fungal succession in mixed temperate forests. New Phytol 176(2):437–447. https://doi.org/10.1111/j.1469-8137.2007.02173.x

Visser S (1995) Ectomycorrhizal fungal succession in jack pine stands following wildfire. New Phytol 129:389–401

Wieder RK, Vitt DH (eds) (2006) Boreal peatland ecosystems. Springer, Berlin Heidelberg. https://doi.org/10.1007/978-3-540-31913-9

Wright HE, Coffin B, Aaseng NE (eds) (1992) The patterned peatlands of Minnesota. University of Minnesota Press, Minneapolis

Wurzburger N, Hartshorn AS, Hendrick RL (2004) Ectomycorrhizal fungal community structure across a bog-forest ecotone in southeastern Alaska. Mycorrhiza 14(6):383–389. https://doi.org/10.1007/s00572-004-0301-x

Wurzburger N, Higgins BP, Hendrick RL (2011) Ericoid mycorrhizal root fungi and their multicopper oxidases from a temperate forest shrub. Ecol Evol 2:65–79

Zhang J, Kobert K, Flouri T et al (2013) PEAR: a fast and accurate Illumina paired-end reAd mergeR. Bioinformatics 30:614–620